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Genetic architecture of growth and early life-history transitions in anadromous and derived freshwater populations of steelhead

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Heritabilities of growth, precocious maturation and smolting were measured in 75 families of juvenile steelhead or rainbow trout *Oncorhynchus mykiss*, progeny of within and between line matings (crosses) of wild, anadromous steelhead and wild, resident (lake) rainbow trout originally derived from the same anadromous stock 70 years earlier. The tagged yearling progeny were combined by line in common freshwater rearing containers and graded into three categories: mature, smolt or rearing (undifferentiated) at age 2 years. Heritabilities of precocious male maturity, smolting and growth were moderate to high, and the genetic correlation between growth and smolting was low. Smolting and precocious male maturity were highly variable among families within lines and significantly different between lines. Each of the four lines produced significant numbers of smolts at age two. Smolting and maturation were negatively genetically correlated, which may explain the persistence of smolting in the lake population despite strong selection against lake smolts; balancing selection on male maturation age may help to maintain variation for smolting. The high heritability of smolting, coupled with the inability of smolts that leave the lake to return to it indicates that the genetic potential for smolting can lie dormant or be maintained through a dynamic interaction between smolting and early maturation for decades despite complete selection against the phenotype. The results have significant implications for the preservation of threatened anadromous stocks in fresh water and the inclusion of resident fish of formerly anadromous populations, currently trapped behind long-standing barriers to migration, as one component of the same population. © 2004 The Fisheries Society of the British Isles

Key words: growth; heritability; maturation; *Oncorhynchus mykiss*; precocious; smolting.

INTRODUCTION

Habitat destruction by logging, hydropower development, mining and urbanization coupled with over-harvest, in the past 100 years have reduced salmonid populations in California, Oregon and Washington to mere remnants of their former abundance (Nehlsen *et al.*, 1991). Steelhead, the anadromous form of *Oncorhynchus mykiss* (Walbaum), has been particularly devastated with two-thirds

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of its evolutionarily significant units (ESUs) considered threatened or endangered under the Endangered Species Act of the United States (Busby *et al.*, 1996). This official legal status for many ESUs has set into motion a series of recovery efforts that include harvest reduction, habitat protection and restoration, and supplementation using conservation hatcheries. Unfortunately, much of the habitat will take decades to restore; therefore, in some situations [*e.g.* Snake River populations of sockeye salmon *Oncorhynchus nerka* (Walbaum)] a portion of the individuals remaining in the wild will require protective custody until the habitat is restored to the point where reintroduction success is likely (Flagg *et al.*, 1995). Protective custody usually involves a fish hatchery with culture raceways or ponds and marine net-pens or pumped seawater tanks for anadromous species. Captive culture is usually very expensive because of the cost required to maintain the large number of animals necessary for large effective breeding populations. For anadromous fishes, the additional burden of providing a saltwater environment for a large portion of the life cycle increases the costs and risks dramatically. In addition to high cost, captive culture, complete with artificial food and human mediated reproduction, can result in genetic change (*e.g.* selection for traits favoured under domestication and reduction in fitness caused by breeding among related individuals) that could be detrimental to recovery of the population when the habitat is ready for re-colonization. Semi-protected natural habitats used to maintain large freely breeding populations (Thrower & Joyce, in press) have many advantages (*e.g.* low cost, natural mate selection and natural foods) over captive culture (Baugh & Decon, 1988). Selection to a different natural environment with potentially negative consequences can still occur, however, and in the case of anadromous fishes lack of the seawater portion of the life cycle might result in significant genetic change associated with migration, saltwater adaptation and marine survival, making the population unsuitable for re-colonization.

In 1996, an attempt was made to exploit an existing situation that might provide insights as to the suitability of freshwater refuges for normally anadromous fishes. In 1926, cannery workers at the Wakefield Fisheries processing plant at Little Port Walter, south-east Alaska, captured juvenile *O. mykiss* from the anadromous portion of Sashin Creek and transplanted them above two 15 m waterfalls into Sashin Lake (Anon, 1939). The lake had been fishless until then and has remained in a pristine state with no human habitation or habitat disruption to the present. In the intervening 70 years, no other introductions of *O. mykiss* to either Sashin Lake or the anadromous portion of Sashin Creek have been documented. Because any fish leaving the lake, such as during a smolting migration, would migrate down over the waterfalls and not be able to return, it was suspected that genes related to smoltification and migration would be heavily selected against in the lake population. It was hypothesized that the proportion of their progeny exhibiting this physiological change (smoltification), when compared in a similar environment with progeny from the anadromous adults of the lower stream, would probably be small to negligible after >15 generations of selection against smolts leaving the lake. It was hypothesized also that the tendency for precocious male maturation might be higher because delayed maturation, when coupled with smolting, would result in failure to reproduce in the lake population.

Comparisons of the phenotypes of specific fitness-based characters (growth, smolting and precocious maturation) expressed within and among families in

each population in a common environment allow for an evaluation of the additive genetic components of each character and of the plasticity in expression of these traits. Such an analysis should provide valuable insight into the effects of long-term freshwater sequestration on variability in these traits and the corresponding consequences for anadromy and viability.

In 1996 wild, maturing, resident rainbow trout *O. mykiss* in Sashin Lake and wild anadromous adults (steelhead) at the Sashin Creek weir were captured and 75 families of pure and reciprocally crossed (hybrid) lines were created. A portion of each family was tagged with passive integrated transponder (PIT) tags at age 1 years and maintained in captivity until age 2 years to determine the influence of 70 years of freshwater confinement in a natural environment on the genetic variables underlying variation in growth, early male maturation and smolting rates.

MATERIALS AND METHODS

GAMETE COLLECTION AND FISH CULTURE

In May and early June, 1996, resident *O. mykiss* adults were captured at the outlet of Sashin Lake (56°22′ N; 134°39′ W) using baited hoop and minnow traps. At the same time, adult anadromous *O. mykiss* were collected at the Sashin Creek weir located in the inter-tidal zone of Sashin Creek. Gametes were collected in plastic bags, placed on ice, and transported to the Little Port Walter Research Station incubation facility. Within 5 h of spawning, gametes were mixed to create groups of fertilized eggs representing pure anadromous, pure resident, and two reciprocally crossed lines (anadromous female × resident male; resident female × anadromous male). All resident fish were killed prior to spawning while most anadromous fish were spawned, alive, from one to several times. Twenty-seven resident females, 26 resident males, and 15 anadromous females and five anadromous males were used to create 75 families. Individual families were kept separate throughout the first year of culture in separate containers (Heintz & Joyce, 1992) and reared under natural light (56° N) and ambient water temperatures. Water for all culture was taken from the upper end of the anadromous portion of Sashin Creek. At age 1 years, *c*. 100 fish from each of 75 families (7424 fish in total) were randomly selected by crowding all family members in a bucket and netting out a portion. They were tagged with PIT tags that enabled individual fish to be identified. The fish were then combined by line into a common rearing container (four lines and four containers) (Martin & Heard, 1987) and cultured for another year. Fish in all containers were fed to satiation from one to three times daily, depending on water temperature, with a commercially available 'trout' diet. Four months after tagging, all fish were individually weighed and measured (fork length, L_F) to determine summer growth. At age 2 years (early June, 1998) the fish were individually examined under anaesthetic. They were weighed, measured (L_F) and classified by life-history type (mature, smolt or undifferentiated). Mature males were identified by generally dark pigmentation and the expression of milt when gentle pressure was applied to the abdomen. Smolts were identified by an overall silvery appearance and a metallic blue-green sheen on the dorsal surface with dark fin tips. Undifferentiated fish were those that retained parr marks, light coloured fins and the normal, cryptic stream colouration.

BREEDING DESIGN AND TRAIT EVALUATION

Variation in size, growth, smoltification and maturation were examined in 6593 progeny of 31 male and 42 female *O. mykiss*. The design constituted a mixture of full-sib, paternal half-sib and maternal half-sib families. Over all lines, the mean number of

females per male was 2·4 (range 1–16) and the mean number of males per female was 1·8 (range 1–4). The distributions of full- and half-sib family sizes are shown in Fig. 1.

Ten traits were evaluated in the 6593 progeny. Measurements of fork lengths (L_F, mm) and mass (g) were made at three points: at age 1 years in June 1997 and October 1997 and at age 2 years in June 1998. From these data, exponential growth rates were estimated in mass ($g\,g^{-1}\,day^{-1}$) for two periods: between June and October 1997 and between October 1997 and June 1998. Finally, smoltification and maturation were assayed at age 2 years for each individual fish in each line.

STATISTICAL ANALYSIS

Variance component estimation

Variance components were estimated with a mixed linear model. For the analysis of genetic and environmental variance components this model has the general form: $y = xb + za + e$, where y is a vector of phenotypic values of individuals, b is a vector of fixed effects, a is a vector of (random) additive genetic effects, x and z are known incidence matrices relating observations in y to effects in a and b, and e is a vector of

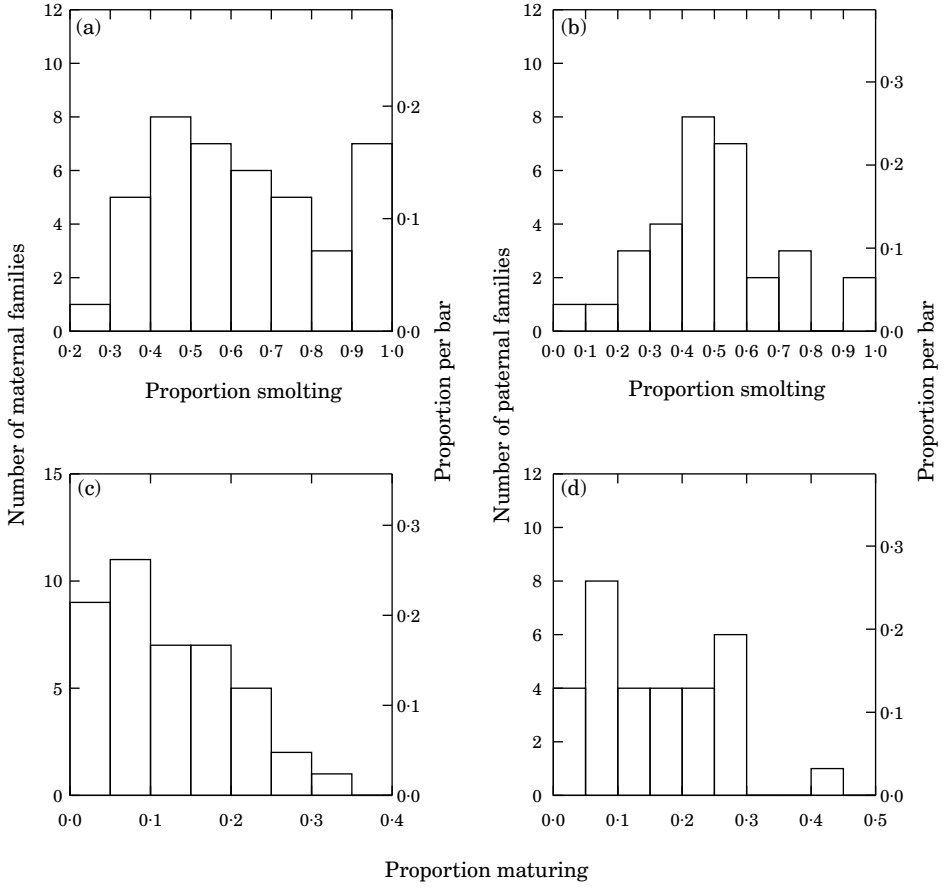

FIG. 1. Distributions of maternal and paternal family sizes for matings among 31 male and 42 female *Oncorhynchus mykiss*. Distributions of proportion smolting at age 2 years among (a) maternal and (b) paternal families and males maturing at age 2 years among (c) maternal and (d) paternal families established from these matings.

residual environmental effects (Henderson, 1984; Sorensen & Kennedy, 1986; Gall *et al.*, 1993). The use of a mixed model requires an assumption that y is a random sample of observations from the population they represent; the distribution of phenotypes in this population is known or assumed to be multivariate normal. In addition, the analysis of mixed models incorporating only additive effects assumes that inheritance is polygenic and that the many constituent genes have small, independent effects on the phenotype (Falconer & Mackay, 1996).

The genetic components of covariance and their derivatives (heritability, h^2 and genetic correlation, r_A) were estimated for each of the traits with restricted maximum likelihood (REML) (Patterson & Thompson, 1971; Harville, 1977; Shaw, 1987). REML was used because variance component estimates derived by least squares (*e.g.* MANOVA) can be biased when family structure is unbalanced and the resulting trait covariance matrices are sparse (Henderson, 1953; Searle *et al.*, 1992). REML produces unbiased variable estimates; in balanced designs, estimates from REML and least squares are equivalent (Searle *et al.*, 1992). Clark (1990) showed empirically that estimates computed by the two methods can correspond well under a fairly typical experimental design.

The genetic model used to estimate variance components was: $y = xb + zs + wd + ie$, where y is the vector of trait values, x is the incidence (design) matrix for the fixed effect of the grand mean, z is the incidence matrix for the random effect of sires, w is the incidence matrix for the random effect of dams and i is the error matrix, and b, s, d and e are vectors containing the effects of these fixed and random factors on the individual phenotype (Hard *et al.*, 1999). The elements of the incidence matrices are 1 if individual i is progeny of sire or dam j and 0 otherwise. This model is easily reformulated in terms of the causal genetic and environmental components of variance and covariance that incorporate the vectors of breeding values (additive genetic effects), dominance deviations, and environmental deviations (Shaw, 1987).

The derivative-free algorithm in the programme DFREML (Meyer, 1997) was used to estimate the genetic variables for each pair of traits because it computes an average information matrix to derive these estimates and their approximate sampling errors for sparse covariance matrices (Johnson & Thompson, 1995). DFREML provided estimates of the variance components and heritabilities and their S.E. for each trait. For the binary traits (smoltification, residency and maturation), the heritability estimates from DFREML to the underlying continuous scale of liability were transformed using the method of Dempster & Lerner (1950): $h^2 = h^2_{0,1} p(1-p) z^{-2}$, where h^2 is the heritability on the underlying scale, $h^2_{0,1}$ is the heritability on the outward binary scale, p is the mean proportion surviving in the population and z is the ordinate on the standardized normal distribution corresponding to p.

The S.E. of these estimates were computed according to the equation (Roff, 1997): $\mathrm{SE}(h^2) = \mathrm{SE}(h^2_{0,1}) p(1-p) z^{-2}$.

Because heritabilities estimated in this way depend on the incidence of the trait (Lynch & Walsh, 1998), an attempt was made to estimate the heritabilities of smoltification and maturation from the incidence of these traits among families under a model of normally distributed liabilities according to the equation: $t = [x_p - x_r \sqrt{1 - (x_p^2 - x_r^2)(1 - x_p \bar{z}_w^{-1})}][\bar{z}_w + x_p^2(\bar{z}_w - x_p)]^{-1}$ where t is the correlation among affected relatives, x_p is the deviation of the threshold in S.D. from the mean liability in the base population (estimated from the incidence of overall smoltification or maturation, Φ_p, and the standard normal distribution), x_r is the deviation of the threshold from the mean liability among affected individuals (estimated from the incidence of among relatives, Φ_r), and z_w is the mean liability of affected individuals in the base population (Falconer, 1965; Hard *et al.*, 2000). For a given overall level of smoltification or maturation, this method provides a test of observed incidence of these traits among affected relatives against that expected if they occurred at random in the population, and provides estimates of genetic variables affecting incidence under the liability model. The heritability (h^2) of liability is computed as $t r^{-1}$, where r is the intraclass correlation (equivalent to the coefficient of relationship among relatives). Mercer & Hill (1984) showed that this equation was a more accurate estimator of

heritability than an estimator based on an ANOVA of binary data followed by a transformation of the resulting observed heritability (computed directly from the data) to a continuous scale (Dempster & Lerner, 1950; Van Vleck, 1972).

Lynch & Walsh (1998) showed that the sampling variance of t can be estimated from:

$$Var(t) \cong [\bar{z}_w^{-1} - t(\bar{z}_w - x_p)]^2 \{[\Phi_p(1-\Phi_p)][N_p p^2(x_p)]^{-1}\} + \{[\Phi_r(1-\Phi_r)][\bar{z}_w^{-2} N_r p^2(x_r)]^{-1}\},$$

where z_w, Φ_p and Φ_r are defined above, N_p and N_r are the sample sizes for the base population and affected relatives, respectively, and $p(x_p)$ and $p(x_r)$ are the heights of the standard normal distribution at the threshold in the base population and among affected relatives, respectively.

DFREML computed the genetic and phenotypic correlations for each combination of traits. Where necessary the environmental correlation between each trait pair, $r_{E(ij)}$, was estimated from the relationship between their phenotypic $r_{P(ij)}$ and genetic correlation $r_{A(ij)}$, according to the equation $r_{E(ij)} = [r_{P(ij)} - r_{G(ij)}(h_i h_j)]\{\sqrt{[(1 - h_i^2)(1 - h_j^2)]}\}^{-1}$ (Falconer & MacKay, 1996).

Bayesian estimation

In an attempt to circumvent issues related to the transformation method a Bayesian method was applied incorporating multivariate mixed models to estimate the variance and covariance components for proportion smolting and proportion maturing directly under a threshold-liability model. The MTGSAM (Multiple Trait Gibbs Sampling for Animal Models) (Van Tassell & Van Vleck, 1995) set of programmes was used to estimate Bayesian posterior means and distributions for variance and covariance components and any fixed and random effects using a Gibbs sampler for analyses involving the threshold traits.

To estimate all the parameters of the model, MTGSAM employs numerical integration methods to generate posterior distributions from prior distributions and the data (Van Tassell *et al*., 1998). Typically, flat prior distributions are used for fixed effects and normal prior distributions for random effects (including variance components). MTGSAM employs Gauss–Seidel iteration to estimate solutions to the mixed model equations (fixed and random effects) using starting values for the variance components before Gibbs samples are generated. Gibbs sampling is a form of data augmentation for categorical traits wherein a value on an unobserved, underlying normally distributed scale of liability (Falconer, 1965) is generated in each round of iteration for each categorical observation. On the liability scale, residual effects are assumed to be distributed normally. They are also assumed to be independent even though individuals can have multiple records. Using this form of iteration the Gibbs sampler generates all genetic effects for an individual, as well as associated uncorrelated random effects simultaneously.

The analyses conducted here used a single Markov Chain Monte-Carlo (MCMC) sample to estimate posterior distributions for each parameter. Priors (initial values) for variance components were the REML point estimates. Gauss–Seidel iterations (1000) computed before initiating Gibbs sampling converged after 11 iterations (convergence criterion $8{\cdot}57589 \times 10^{-4}$), and each Gibbs sampling chain was run for 150 000 rounds with the first 25 000 rounds discarded for 'burn-in'. The length of the 'burn-in' period was determined from subjective evaluation of plots of values from the chain. Thinning of the chains used the methods described in Van Tassell *et al*. (1998), and was based on evaluating and reducing the lag correlations computed from the chains.

The MTGSAM programmes do not compute Bayesian posterior densities for estimated parameters; to accomplish this the programme BOA (Bayesian Output Analysis) (Smith, 2003) was used running in the *R* statistical environment (under GNU General Public License). BOA was used to evaluate convergence of the chains generated by MTGSAM with several diagnostic tests (Geweke, 1992; Raftery & Lewis, 1992*a*, *b*; Brooks & Gelman, 1998) and compute Bayesian credible intervals for posterior means from the estimated posterior distributions. BOA estimates Bayesian Highest Probability

Density (HPD) intervals using the algorithm of Chen & Shao (1999), assuming a unimodal marginal posterior distribution. The HPD interval is the shortest of the Bayesian posterior intervals, and it represents the interval within which the posterior mean lies with probability $(1-\alpha)\%$.

RESULTS

There were substantial differences in size of adult spawners between the anadromous and resident forms and also in the resulting eggs and emergent fry (Thrower *et al.*, 2004). The majority of the difference in fry size between lines was eroded by higher growth rates by the progeny of resident females so that by age 2 years the lines were indistinguishable in mass In the first 3 months after tagging, 6% of the fish died and *c.* 4% of the PIT tags were lost. Over the next 9 months there was <0·4% tag loss and mortality, combined. No disease outbreaks were detected during culture. Effective survival rate of PIT tagged fish, including tag loss, was 89·5%. Final culture densities in the raceways at age 2 years varied from $3{\cdot}24\,\mathrm{kg\,m^{-3}}$ for the resident × resident line to $6{\cdot}49\,\mathrm{kg\,m^{-3}}$ for the anadromous × anadromous line. The resident female × anadromous male line survived significantly higher (93·6%) (ANOVA, $n=75$; $P=0{\cdot}001$) than the other lines that were not significantly different from each other with a combined mean of 87·7%.

PATTERNS OF SIZE, GROWTH, SMOLTIFICATION AND MATURATION

Trait distributions and variation among lines and families

Table I provides the summary statistics for the 10 *O. mykiss* traits in the analysis. Distributions of L_F and mass in each sample, across lines and families, are given in Fig. 2; corresponding distributions for growth rates at age 1 years and between ages 1 and 2 years by lines are depicted in Figs 3 and 4, respectively. Fork lengths, mass and growth rates differed significantly among the four lines (MANOVA; Wilks' $\lambda_{24,6508}$, $P<0{\cdot}001$). The univariate *F*-tests are summarized in Table II; these tests indicate that, with the exception of masses sampled in October 1997 and June 1998, the lines differed for all size and growth traits. Pair-wise comparisons for the traits showing significant variation among lines indicated the following patterns ($P<0{\cdot}05$ after Bonferroni correction for multiple tests; $A=$ anadromous parent, $R=$ resident parent): June 1997 L_F (LG1): R female × R R male < A female × R male, R female × A male, A female × A male; June 1997 mass (WT1): R female × R male < A female × R male < R female × A male, A female × A male; October 1997 L_F (LG2): R female × R male, A female × R male < R female × A male, A female × A male; June 1998 L_F (LG3): R female × R male, A female × R male < R female × A male, A female × A male; age 1 year growth (GR1): A female × A male < R female × A male < A female × R male < R female × R male; age 1–2 year growth (GR2): A female × A A male < A female × R male, A female × R male, R female × R male.

Collectively, these results indicate that progeny of resident parents tended to be smaller than those of anadromous parents, but progeny of resident parents had higher growth rates, especially initially. The line, however, explained >5%

TABLE I. Summary statistics and estimates of variance components and heritabilities (h^2) for 10 traits measured in the *Oncorhynchus mykiss* population: SMO, proportion smolting at age 2 years; MAT, proportion maturing at age 2 years; LG1, fork length (mm) at sampling in June 1997 (age 1 year); WT1, mass (g) in June 1997 (age 1 year); LG2, fork length in October 1997 (age 1 year); WT2, mass in October 1997 (age 1 year); LG3, fork length in June 1998 (age 2 years); WT3, mass in June 1998 (age 2 years); GR1, exponential daily growth in mass ($g\,g^{-1}\,day^{-1}$) between June and October 1997; and GR2, exponential daily growth in mass ($g\,g^{-1}\,day^{-1}$) between October 1997 and June 1998. Except for SMO and MAT, genetic variables were estimated with the restricted maximum likelihood (REML) model; those for SMO and MAT were estimated with a Bayesian algorithm under a threshold-liability model (see text). n, total number of records; V_P, phenotypic variance; CV, coefficient of variation (%); V_A, additive genetic variance; h^2, narrow-sense heritability; SE(h^2), approximate S.E. of h^2

Trait	n	Mean	V_P	CV	V_A	h^2	SE(h^2)
SMO	6593	0·610	0·238	79·984	0·106	0·726	0·134
MAT	6593	0·123	0·108	267·407	0·055	1·149	0·276
LG1	6592	74·515	62·301	10·593	36·134	0·580	0·080
WT1	6586	4·491	2·308	33·828	1·366	0·592	0·081
LG2	6569	144·236	316·756	17·798	180·234	0·569	0·078
WT2	6573	38·495	191·443	35·943	108·931	0·569	0·078
LG3	6582	195·179	588·501	12·429	340·742	0·579	0·079
WT3	6582	80·852	616·907	30·720	406·542	0·659	0·083
GR1	6570	0·020	0·6E−5	12·434	0·5E−5	0·737	0·094
GR2	6565	0·003	0·1E−5	25·553	0·1E−7	0·209	0·042

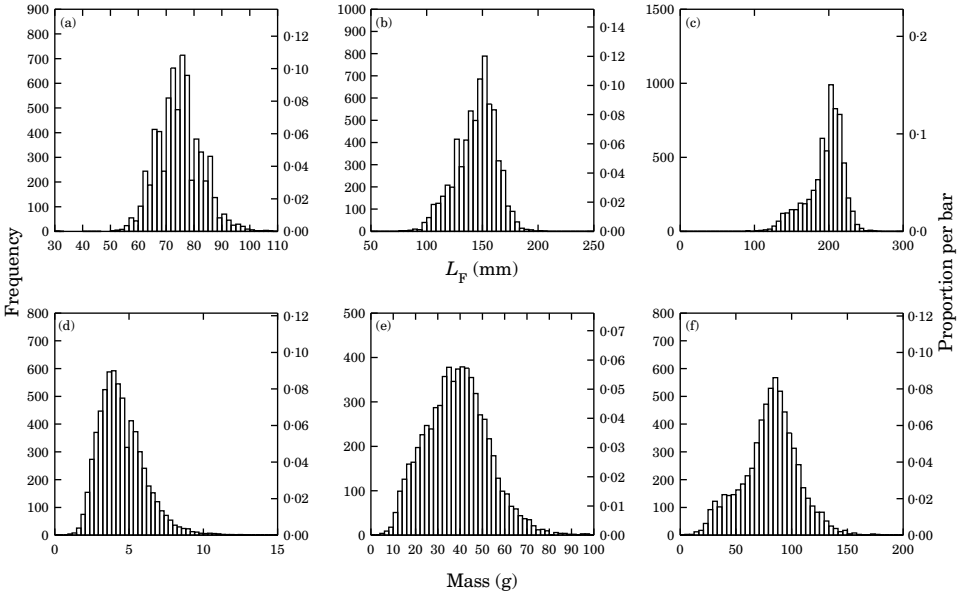

FIG. 2. Distributions (families and crosses combined) of fork lengths for *Oncorhynchus mykiss* sampled at age 1 year in (a) June 1997 and (b) October 1997, and at age 2 years in (c) June 1998 and masses for fish sampled at age 1 year in (d) June 1997 and (e) October 1997, and at age 2 years in (f) June 1998.

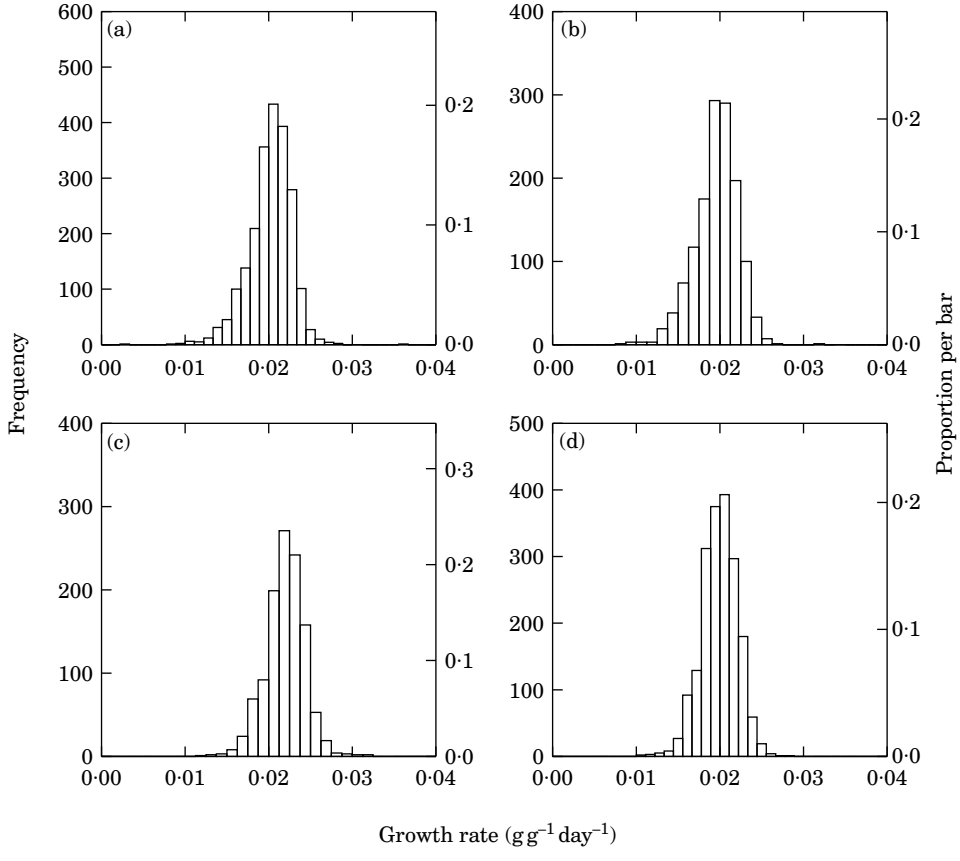

FIG. 3. Distributions (families combined) of growth rates in age 1 year *Oncorhynchus mykiss* between June and October 1997 for progeny of the four crosses: (a) anadromous female × anadromous male, (b) anadromous female × resident male, (c) resident female × resident male and (d) resident female × anadromous male.

of the total variance for only initial fork lengths, masses and growth rates; paternal family typically explained <1% of the total variance in all traits (Table II and Figs 3 and 4).

Overall, when lines and families were pooled, smolts and mature fish had the highest (and equivalent) mean growth rates. Undifferentiated fish grew at a significantly lower rate. Fish destined to smolt or mature were significantly larger at tagging (76·1 mm) than undifferentiated fish (70·3 mm) (ANOVA, $n = 6593$, $P < 0{\cdot}001$). For fish destined to become smolts, growth rates were significantly higher (ANOVA, $n = 75$, $P < 0{\cdot}001$) in the pure resident fish (0·856% body mass day^{-1}) and lower and equivalent in the other lines (0·814% body mass day^{-1}). For fish destined to become mature at age 2 years, the pure lines grew equivalently (0·762% body mass day^{-1}) and significantly (ANOVA, $n = 75$, $P < 0{\cdot}001$) faster than the hybrid lines, which were not different from each other (0·708% body mass day^{-1}). Growth of undifferentiated fish was

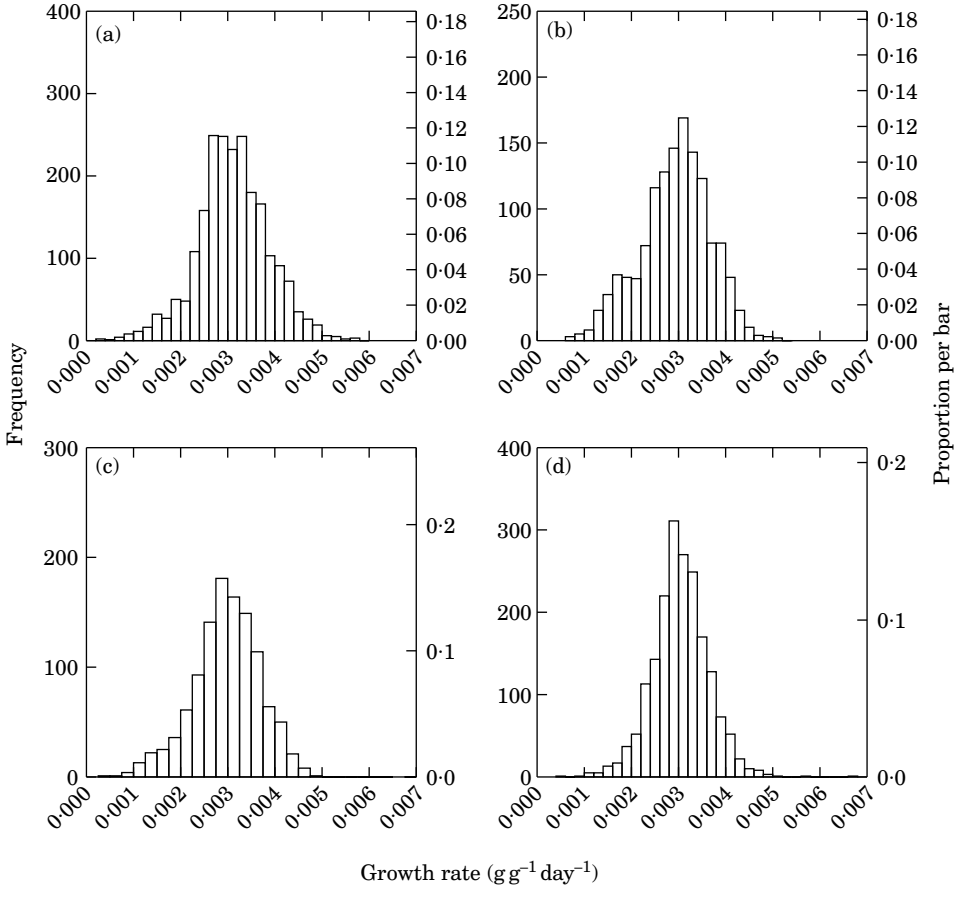

FIG. 4. Distributions (families combined) of growth rates between age 1 and age 2 years in *Oncorhynchus mykiss* between October 1997 and June 1998 for the four crosses: (a) anadromous female × anadromous male, (b) anadromous female × resident male, (c) resident female × resident male and (d) resident female × anadromous male.

significantly ($P < 0{\cdot}005$) higher in the pure resident line (0·823% body mass day^{-1}) than in the other three lines, which were not different from each other (0·757% body mass day^{-1}).

The distributions of proportion smolting and maturing among maternal and paternal families are shown in Fig. 5. Smolting proportion was highest in the resident female × anadromous male hybrid line (0·71) and lowest in the pure resident line (0·44). Overall range of smolting proportion among all families varied from 0·02 to 0·99. Precocious maturation was also highly variable among families and varied from 0 to 0·50 (or 100% of the males assuming a sex ratio of 1 : 1). Precocious maturation had the highest family average in the anadromous female × resident male hybrid line (0·16) and lowest in the resident female by anadromous male hybrid line (0·10). The proportion of fish that did not smolt or mature was also highly variable among families and lines and varied from 0·01 to 0·92 and was highest in the pure resident line (0·41) and lowest in the resident female × anadromous male line (0·19).

TABLE II. Univariate *F*-tests for (a) effects of line (fixed effect) and (b) father (random effect) on size (fork lengths = LG1–LG3; masses = WT1–WT3) and growth (GR1 and GR2). See text for discussion and results of multivariate analysis. %TSS = % reduction in total sum of squares

(a) Effect of line Source	SS	d.f.	MS	*F*	%TSS	*P*
LG1	29141·730	3	9713·910	167·988	7·715	<0·001
Error	377713·262	6532	57·825			
WT1	853·003	3	284·334	130·698	6·005	<0·001
Error	14210·400	6532	2·176			
LG2	12578·747	3	4192·916	13·314	0·612	<0·001
Error	2057090·202	6532	314·925			
WT2	177·678	3	59·226	0·309	0·014	0·819
Error	1250025·494	6532	191·369			
LG3	120304·946	3	40101·649	70·470	3·237	<0·001
Error	3717077·952	6532	569·057			
WT3	3086·454	3	1028·818	1·669	0·077	0·171
Error	4026201·869	6532	616·381			
GR1	0·004	3	0·001	246·530	10·811	<0·001
Error	0·037	6532	<0·001			
GR2	<0·001	3	<0·001	10·460	<3·000	<0·001
Error	0·003	6532	<0·001			
(b) Effect of father (paternal family) Source	SS	d.f.	MS	*F*	%TSS	*P*
LG1	387·523	1	387·523	6·702	0·103	0·010
Error	377713·262	6532	57·825			
WT1	9·925	1	9·925	4·562	0·070	0·033
Error	14210·400	6532	2·176			
LG2	3740·862	1	3740·862	11·879	0·182	0·001
Error	2057090·202	6532	314·925			
WT2	855·978	1	855·978	4·473	0·069	0·034
Error	1250025·494	6532	191·369			
LG3	1634·070	1	1634·070	2·872	0·044	0·090
Error	3717077·952	6532	569·057			
WT3	46·657	1	46·657	0·076	0·001	0·783
Error	4026201·869	6532	616·381			
GR1	<0·001	1	<0·001	0·970	<2·703	0·325
Error	0·037	6532	<0·001			
GR2	<0·001	1	<0·001	38·890	–	<0·001
Error	0·003	6532	<0·001			

Relationships between smoltification or maturation and size and growth

Proportion smolting at age 2 years tended to increase with both mass at age 1 year (October 1997) and growth rate between ages 1 and 2 years in all lines (Fig. 6), but none of the individual regression slopes (*b*) were significant. The

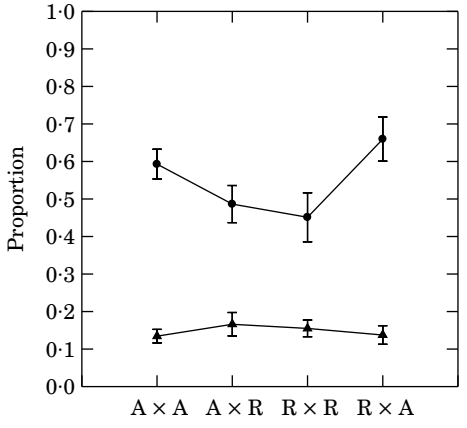

FIG. 5. Proportions (means ± S.E.) *Oncorhynchus mykiss* smolting (•) and maturing (▲) at age 2 in the four lines. A × A, anadromous female × anadromous male; A × R, anadromous female × resident male; R × R, resident female × resident male; R × A, resident female × anadromous male.

regression across lines of proportion smolting on weight was not significant ($r^2 = 0{\cdot}02$, $b = 0{\cdot}002 \pm 0{\cdot}002$, $F_{1,65}$, $P = 0{\cdot}240$). The regression across lines of proportion smolting on growth rate was highly significant, although the positive relationship was weak ($r^2 = 0{\cdot}12$, $b = 107{\cdot}902 \pm 35{\cdot}607$, $F_{1,65}$, $P = 0{\cdot}004$).

The proportion maturing at age 2 years tended to decrease with both mass at age 1 years and growth rate between ages 1 and 2 years in all lines (Fig. 6), the regressions were significant for only two lines: anadromous females × resident males and resident females × anadromous males. The regression across lines of proportion maturing on mass was not significant ($r^2 = 0{\cdot}017$, $b = -0{\cdot}001 \pm 0{\cdot}001$, $F_{1,61}$, $P = 0{\cdot}313$). The regression across lines of proportion maturing on growth rate was highly significant, although the negative relationship was also weak ($r^2 = 0{\cdot}103$, $b = -39{\cdot}483 \pm 15{\cdot}057$, $F_{1,61}$, $P = 0{\cdot}010$).

GENETIC COMPONENTS OF VARIANCE

REML estimates

The maximum likelihood estimates of the variance components for the 10 traits indicated that all traits showed appreciable variation among half- and full-sibs (Table I). Heritability estimates for fork length and mass generally ranged between 0·5 and 0·7; those for growth rates varied from *c.* 0·75 during summer in age 1 fish year to *c.* 0·20 for growth after that period. The heritability under a continuous-distribution model for smoltification at age 2 years was 0·45, suggesting that about half the observed variability in smolting was due to covariance of half-sibs and, therefore, additive genetic variation for propensity to smolt. The continuous-distribution heritability estimate for maturation at age 2 years was 0·44, suggesting that about half of the expressed variability in maturity was due to additive genetic variation for propensity to mature.

The patterns of phenotypic and genetic correlations among the traits showed some evidence of dissimilarity, but only a few of the genetic correlations differed

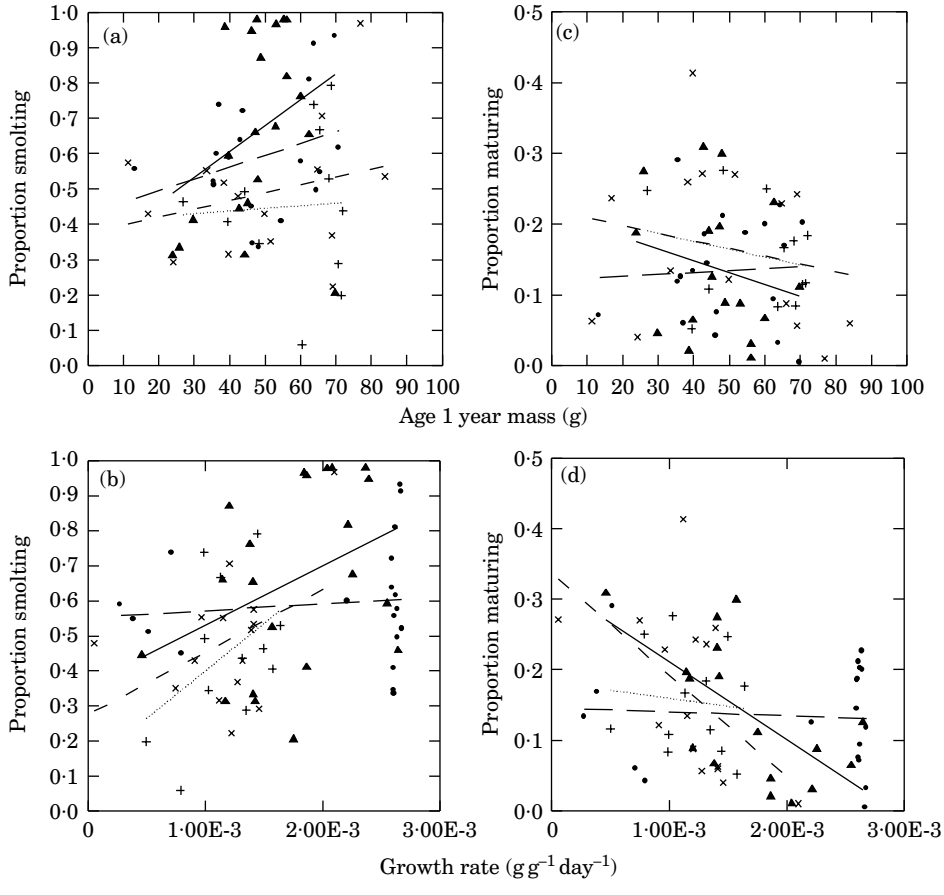

FIG. 6. The relationship between the proportion (a) smolting at age 2 years and age 1 year mass (October 1997), (b) smolting at age 2 years and growth rate between age 1 and 2 years, (c) maturing at age 2 years and age 1 year mass (October 1997) and (d) maturing at age 2 years and growth rate between age 1 and 2 years in four lines (•—, anadromous females × anadromous males; ×—, anadromous females × resident males;+– –, resident females × resident males; ▲·····, resident females × anadromous males) of *Oncorhynchus mykiss*. The lines were drawn to show trends.

significantly from zero (Table III). Initial mass at age 1 year was positively genetically correlated with age-1 year mass, sampled 4 months later ($r_A = 0{\cdot}71$); its correlation with mass at age 2 years was not different from zero, although the point estimate was 0·56. Initial mass was negatively genetically correlated with proportion maturing at age 2 years (−0·18). The proportion smolting at age 2 years and the proportion maturing at age 2 years were negatively genetically (−0·44) as well as phenotypically (−0·47) correlated. Phenotypic correlations among the size and growth traits were moderate to large; the largest correlations occurred between the sizes (0·56–0·93) and between initial growth rate and the later masses (0·43–0·63). These correlations were all positive and generally similar to the corresponding phenotypic correlations. The negative genetic correlation between the proportion smolting and the proportion maturing at age 2 years indicates the likely presence of antagonistic pleiotropy (or possibly linkage)

TABLE III. Genetic and phenotypic correlation matrices estimated for seven of the 10 traits measured in the *Oncorhynchus mykiss* population, focusing on relationships between key developmental stages, mass and growth in mass: SMO, proportion smolting at age 2 years; MAT, proportion maturing at age 2 years; WT1, mass (g) in June 1997 (age 1 years); WT2, mass in October 1997 (age 1 year); WT3, mass in June 1998 (age 2 years); GR1, exponential daily growth in mass between June and October 1997; GR2, exponential daily growth in mass between October 1997 and June 1998. Parameters were estimated with the REML model. Above diagonal (all entries on diagonal are 1·000), phenotypic correlations; below diagonal, genetic correlations. Genetic correlations in bold differ by >2S.E. from zero; S.E. for those correlations in italics could not be estimated

	SMO	MAT	WT1	WT2	WT3	GR1	GR2
SMO	1·000	−0·468	−0·145	−0·280	−0·542	−0·281	−0·124
MAT	**−0·441**	1·000	−0·107	−0·126	0·215	−0·049	0·473
WT1	0·012	**−0·184**	1·000	0·774	0·589	−0·098	−0·384
WT2	−0·312	−0·069	**0·706**	1·000	0·857	0·492	−0·482
WT3	−0·482	0·200	0·563	*0·934*	1·000	0·541	0·016
GR1	*−0·431*	*0·103*	*−0·170*	*0·426*	*0·628*	1·000	−0·222
GR2	*−0·086*	*0·511*	*−0·419*	*−0·219*	*−0·083*	*−0·083*	1·000

between these traits (pleiotropy, or multiple gene effects, and linkage between loci are the most common causes of genetic correlation; Lynch & Walsh, 1998). The genetic correlations among the remaining pairs of traits were smaller and, generally, not different from zero (Table III).

Liability-threshold model estimates

The h^2 of maturation at age 2 years on the observed scale, estimated from the variance components, was $0{\cdot}44 \pm 0{\cdot}11$. Applying the transformation to the continuous scale yielded an estimate of the h^2 of liability to mature that was considerably higher: $1{\cdot}15 \pm 0{\cdot}28$. This substantially larger, and clearly infeasible, estimate undoubtedly reflects in part the non-linear dependence of the transformation on the incidence of maturation (0·12) (Lynch & Walsh, 1998; Hard *et al.*, 2000). To attempt to provide an independent estimate of this h^2 from the underlying liabilities in progeny of affected mothers, the frequency of maturation at age 2 years in affected full-sib families was compared to that in the population at large (because all half-sib families produced maturing fish, it was not possible to apply this method using half-sib families). The estimate of h^2 from this method was $0{\cdot}05 \pm 0{\cdot}02$, based on incidence of maturation in full-sib families. Although different from zero, it is considerably smaller than the REML estimate. Nevertheless, because the estimate is based on incidence in full-sibs, it is a broad-sense estimate, one affected by nonadditive genetic and environmental sources of variation. It is not affected by the frequency of maturation, however, and is probably closer to the true value of the heritability than the transformed REML estimate.

Bayesian estimates

Bayesian point estimates for heritabilities of, and genetic correlations between, proportion smolting (SMO) and proportion maturing (MAT) at age

2 years, are presented in Table IV. Posterior densities are shown in Fig. 7. Table IV also provides 95% highest posterior density (HPD) intervals for the posterior means. The transformed heritabilities from the REML analyses were 0·73 and 1·15, respectively. The transformed heritability estimate was somewhat higher than the threshold estimate for SMO, but for MAT, the transformed estimate was much higher, 225% of the threshold estimate. Collectively, the heritabilities indicate that substantial genetic variation existed for both SMO and MAT. The posterior distributions for both heritabilities were somewhat symmetric but showed several outliers in both tails (Fig. 7) that contributed to the wide HPD intervals (Table IV).

The two traits were negatively genetically correlated. The mean posterior estimate of genetic correlation between SMO and MAT was −0·84 for the threshold model; the REML estimate was −0·44. Although the estimates from the linear and threshold models differed, the 95% HPD interval from the threshold model is large and includes the REML estimate. The negative genetic correlation between the traits indicates that SMO was related to MAT and that selection to increase SMO would produce an antagonistic correlated response to reduce MAT. The HPD intervals for these estimates were broad and the posterior distribution for the genetic correlation showed evidence of more than one mode, indicating poor precision for these parameters. The wide intervals result, in part, because of the data structure. Monte-Carlo estimates of S.D. were 3·43 for the heritability of SMO, 3·25 for the heritability of MAT, and 3·78 for the genetic correlation between them.

DISCUSSION

Substantial differences in size, growth, smoltification and maturation (at age 2 years) were found among the four lines (Table II and Fig. 6). These results suggest that size and growth thresholds for smoltification and maturation differ between lines, underscoring a marked phenotypic plasticity that the population harbours for three distinct developmental pathways: smolting, maturing or continuing to grow without undertaking either process. The patterns illustrated in Figs 5 and 6 show that much of this plasticity in growth, smoltification and maturation is expressed between the different lines. In particular, the relationship between smolting or maturing and growth rate varies among fish with

TABLE IV. Genetic parameters estimated for the two threshold traits: proportion smolting at age 2 years (SMO) and proportion maturing at age 2 years (MAT), under a threshold-liability model. Parameters were estimated with a Bayesian algorithm (MTGSAM, see text). On diagonal, heritabilities; below diagonal, genetic correlation. Highest posterior density (HPD) intervals for the estimates ($\alpha < 0{\cdot}05$) include zero and are in parentheses

	SMO	MAT
SMO	0·560 (−1·537–4·339)	
MAT	−0·841 (−2·700–4·872)	0·511 (−3·980–2·240)

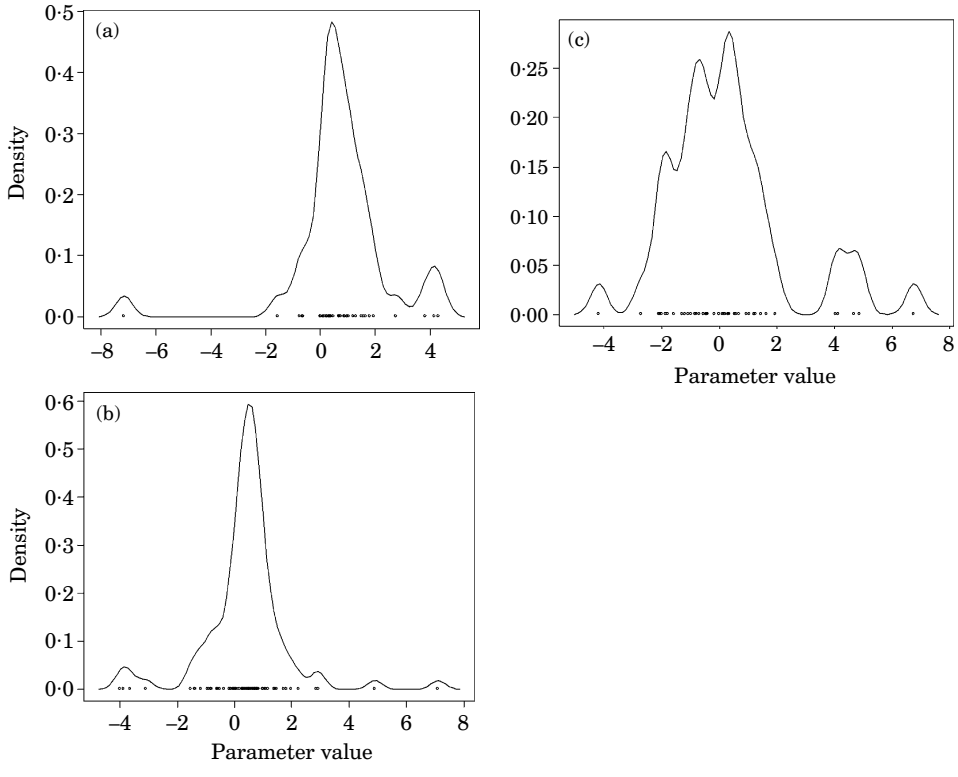

FIG. 7. Bayesian posterior density estimates of heritabilities for (a) proportion smolting and (b) maturing at age 2 in *Oncorhynchus mykiss* and (c) the genetic correlation between these traits.

parents expressing contrasting life histories. The evidence of variability underlying differences among families within lines in size, growth, and rates of smoltification and maturation indicates, moreover, that this plasticity has a substantial genetic basis.

The heritabilities of the morphological and developmental traits in these populations of *O. mykiss* indicate that all of them are capable of responding to selection (Tables I and III). Despite the difficulty in estimating some of the parameters for proportion smolting or maturing at age 2 years, the large heritabilities for all the traits (size, growth, smoltification and maturation) reflect additive genetic variation sufficient for rapid selection response. Proportion smolting and proportion maturing at age 2 years both showed variation that was expressed largely among lines; nevertheless, the variability among families grown under common culture conditions indicates that both traits are influenced by appreciable underlying genetic variability in these populations.

The phenotypic and genetic patterns among the traits are depicted graphically in Fig. 8. Where they could be estimated reliably, the genetic correlations between size and growth indicate that higher growth rates or size at age 2 years could evolve rapidly in this population if conditions permit. For example, large positive genetic correlations occurred between the masses sampled at age 1 years (after the summer growing season) and at age 2 years. These results are

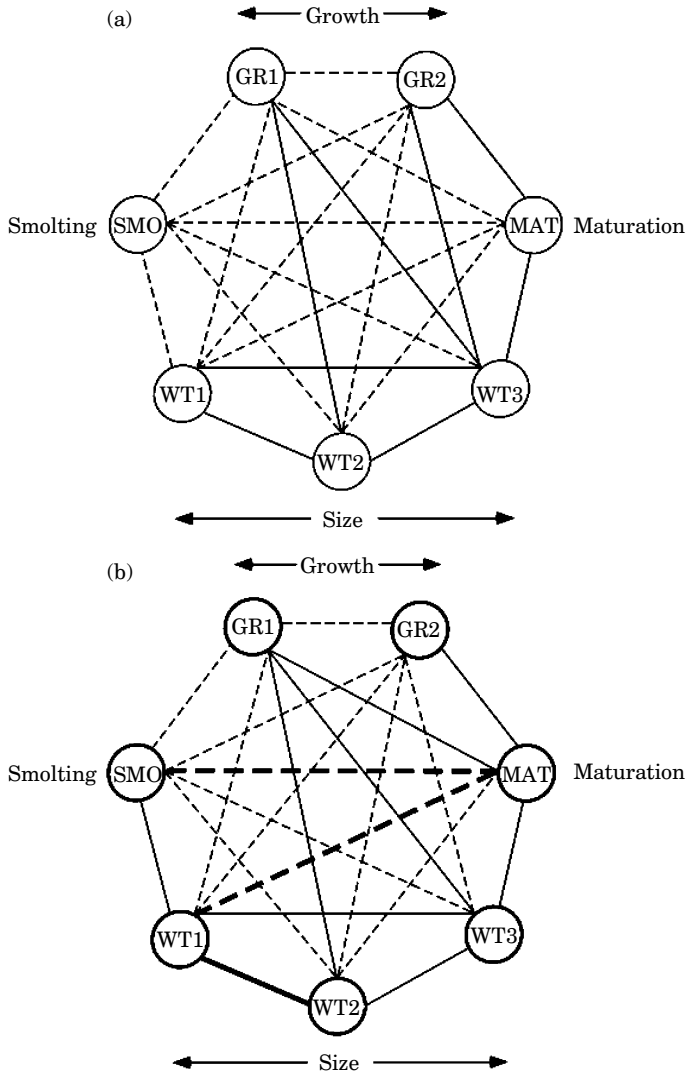

FIG. 8. Graphical representation of phenotypic correlations among (a) and heritabilities (h^2) for and genetic correlations among (b) seven of the 10 traits measured in the *Oncorhynchus mykiss* population, focusing on relationships between key developmental stages, size and growth: SMO, proportion smolting; MAT, proportion maturing; WT1, mass (g) in June 1997; WT2, mass in October 1997; WT3, mass in June 1998; GR1, exponential daily growth in mass between June and October 1997; GR2, exponential daily growth in mass between October 1997 and June 1998. Parameters were estimated with the REML model. Heritabilities for SMO and MAT are based on a threshold-liability model. Solid circles for all traits in (b) indicate heritability estimates significantly >0 ($\alpha < 0{\cdot}05$). —, positive genetic correlations; ----, negative genetic correlations; ——— and - - -, estimates significantly different from 0 ($P < 0{\cdot}05$).

consistent with those obtained by Fishback *et al.* (2002) who measured high genetic correlations for L_F, mass and condition factor using multiple trait REML for a farmed population of rainbow trout. The genetic relationship between mass at age 1 years and maturation at age 2 years was strongly

negative; that between age 1 year mass and smoltification at age 2 years was not different from zero (Fig. 8). The genetic relationship between proportion smolting and proportion maturing was highly negative. These relationships strongly imply that a common set of genes influences expression of growth and size, and the generally good correspondence with the phenotypic correlations among the traits indicates that observed patterns of growth and size under the culture conditions employed in this study are reasonable proxies for the underlying genetic relationships. The strong negative phenotypic and genetic relationships between proportion smolting and maturing at age 2 years identify two prominent consequences. Clearly, conditions that favour increased smolting will tend to reduce the rate of maturation (at age 2 years), and the converse is also true. In addition, the likely antagonistic pleiotropy that underlies genetic control of these traits has uncertain implications for viability of the lake population. Continued selection against smolting may lead to a decrease in age at first maturation, with possible consequences for growth rate due to the genetic correlation between maturation and growth. Schmidt & House (1979) found a high degree of variation in precocious maturation in a survey of hatchery steelhead populations in Idaho (western U.S.A.) and related age, temperature and photoperiod to some of this variation. They also concluded that the maturing males were lost to the smolting populations. Regardless of the implications, it is clear that conditions that fluctuate and favour smoltification or maturation to different degrees in different years will tend to maintain genetic and phenotypic variability for these traits in the population.

The significant differences in growth, smolting and maturation rates between families within lines indicates that significant genetic variation in these traits exists in the original steelhead donor stock and continues to exist in the stock that was transplanted to Sashin Lake. It is remarkable that such high levels of variation were observed given the high heritability of the characters examined and the relatively small number of adult males available for the experiment from the pure anadromous population. The lake population produced lower proportions of smolts but still retains a large amount of variation between families. The selection coefficient for smolting in this population would be expected to be very large and negative because the phenotypic expression of this physiological process includes downstream migration, which in this case, results in a loss of those genotypes from the population. Because high variation for this trait remains, this suggests some form of balancing selection is occurring in the lake population, one that maintains a selective advantage for fish possessing the genes associated with smolting (*e.g.* high spring growth rates) while the phenotypic expression of smolting and the associated downstream migration is rarely manifested.

The results of this study indicate that after 70 years of freshwater residency, a formerly anadromous, wild, freely breeding population of *O. mykiss* has retained large amounts of genetic variability associated with growth, precocious maturation and smolting despite complete selection against the phenotypic expression of at least one of the fitness related characters (smolting migration) critical for the reestablishment of an anadromous population. Contrary to expectations, it appears that the dynamic interactions of season specific growth rates, early maturation and smolting have maintained substantial genetic variation in these critical life-history traits. The results of Thrower & Joyce (in press),

however, indicated that the marine survival of the smolts of the lake-derived fish is poor relative to the smolts derived from anadromous parents. Consequently, key genetic factors associated with marine survival do not appear to be closely linked to freshwater growth, precocious maturation or smolting in the lake population. Thrower *et al.* (2004) speculated that the poorer marine survival could be due to the lower overall genetic variability of this population associated with a founder effect at stocking. Selection in the marine environment, however has been operative over the last 70 years (*c.* 12–14 generations) in the anadromous population, which has maintained a connection with changing marine conditions, the resident population in the lake has not had. Genes associated with marine survival may have been 'archived' in the lake population (perhaps through linkage with selectively positive traits) without access to adaptive marine selection. It is possible, therefore, that both genetic impoverishment (in terms of alleles influencing marine survival) and lack of reinforcing selection on migratory behaviour could be responsible for the reduced marine performance. In formerly anadromous populations maintained in freshwater habitats for extended periods, if sufficient genetic variability has been maintained for migratory behaviour and other factors contributing to marine survival, selection upon return to marine environments should improve marine survival rates.

Although these interpretations of the data seem to be probable explanations, several conditions existed with the experiment that could have influenced the outcome. Density during culture has been shown to affect growth rates in rainbow trout (Refstie, 1977) and densities were variable between lines in this experiment that might have influenced growth rates. The densities used in this experiment were very low however (maximum $6{\cdot}5\,\mathrm{kg\,m^{-3}}$), when compared to normal production culture densities ($>30\,\mathrm{kg\,m^{-3}}$), specifically to minimize this influence. Blanc & Poisson (2003) found effects of family by family interactions on growth in the same containers during their first year. Isolation between lines was maintained in this experiment and family by family interactions were avoided in the first year, however families within lines were combined in the second year and could have impacted these results. Rowe & Thorpe (1990) found that reduction in feeding and growth at certain times of the year was instrumental in reducing precocious male maturity while fast spring growth increased precocious male maturity in Atlantic salmon *Salmo salar* L. While environmental conditions were similar in all lines in this experiment, the general water temperature regime during the tests might have affected maturation rates and the phenotypic expression of smolting. This might have affected heritability estimates although the affects on the lines would probably have been similar. Specifically with regard to smolting, however, all the fish that did not smolt were retained in fresh water for another year and evaluated for smolting at age 3 years (unpubl. data). Only 93 fish smolted at age 3 years (compared to >4000 at age 2 years), none of which had been mature males at age 2 years, a pattern that indicates that overall growth, at least, did not significantly inhibit age 2 years smolting. High lipid levels, which might be more common in a hatchery environment, however, may have stimulated high rates of early male maturity (Shearer & Swanson, 2000; Larsen *et al.*, 2004) and subsequently reduced smolting rates. The maintenance of high levels of variability for growth, precocious maturation and smolting in the Sashin Lake population might not be

easily reproduced in other places. Selection in refuge habit could also have undesirable effects. Differences in environmental conditions might stimulate the phenotypic expression of smolting to a high degree and effectively remove those genes from the population (through emigration) thus limiting its utility for reintroduction. Alternatively, Zaugg & Wagner (1973) demonstrated significant impacts of temperature and photoperiod on smoltification in steelhead. They found that temperatures $>12{\cdot}5^{\circ}$ C during the normal migration period (May to June) reduced adenosinetriphosphatase (ATPase) levels and the downstream migration associated with smolting. These results would seem to indicate that certain natural environments that develop high spring temperatures might inhibit the development of smoltification almost completely and thus eliminate that particular type of genetic loss from the population.

Given the above qualifications, the judicious use of freshwater sequestration merits consideration as a temporary component of a comprehensive strategy for the maintenance of endangered anadromous populations of *O. mykiss* in cases where the likelihood of rapid restoration of freshwater habitats for anadromous fish is low.

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